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Oxygen Requirements of Embryos and Larvae of the Largemouth Bass, 'Micropterus salmoides' (Lacpede)

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16. ABSTRACT

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Embryos	Avoidance response	06F
Larvae	Largemouth bass	06K
Respirator	Stress physiology	06P
Hypoxia	Year-class strength	06S
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Oxygen requirements of embryos and larvae of the largemouth bass, *Micropterus salmoides* (Lacépède)

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(*Accepted 20 April 1976*)

Starting with the second day after fertilization, largemouth bass embryos and larvae became increasingly sensitive to oxygen deficiency until the sixth day of life. On this day few survived exposure to 1 mg O_2/l for 3 h at 20° C; many were damaged at 2 mg/l, but not at 2·5. Death was by asphyxiation or by starvation resulting from an apparent inability to close the lower jaw. On the seventh day the larvae became more resistant again, possibly because opercular movement began on that day. At 25° C the effects of reduced oxygen concentration were intensified, and even a concentration of 2·5 mg/l became lethal in 3 h. At 3 mg O_2/l and 20° the normally quiescent yolk-sac larvae became very active and swam vertically to at least 5 or 6 cm above the substrate; 4 and 5 mg/l had this effect at 23–24°. This behaviour could result in losses by predation and displacement from the nest.

I. INTRODUCTION

Kramer & Smith (1962) concluded the year-class strength of a population of largemouth bass (*Micropterus salmoides*) was set during the first 2 weeks of life. Low oxygen concentrations are known to cause high mortality among largemouth embryos and larvae (Carlson & Siefert, 1974; Dudley & Eipper, 1975), and Dudley & Eipper (1975) have considered oxygen deficiency as a possible factor in setting year-class strength. The present study was undertaken to test this possibility.

It has been suggested for a number of species that sensitivity to oxygen deficiency is especially great at the time of hatching (Lindroth, 1942; Gottwald, 1965), and Dudley & Eipper (1975) found the largemouth bass to be more sensitive at hatching than during the stages preceding it. There are indications, however, that sensitivity increases after hatching. Carlson & Siefert (personal communication) found largemouth bass mortality at 1·4–1·7 mg O_2/l was much higher several days after hatching than at the time of hatching or on the day following it, and Brungs (1971) found that fathead minnow, *Pimephales promelas*, fry were unable to survive for more than a few days at an oxygen concentration at which hatching was successful. Larval as well as embryonic stages have therefore been subjected to oxygen deficiency. The oxygen concentrations tested and the temperatures were within ranges to be found in the largemouth bass habitat.

II. MATERIAL AND METHODS

The tests were conducted in screen-bottomed trays 15×3×7 cm high (Fig. 1). The screen was of 40-mesh stainless steel, the sides and ends were of 3-mm acrylic plastic sheet,

and the top was open. Each tray was supported above the bottom of an outer chamber of acrylic plastic so that continuously flowing water, entering by way of a needle valve, passed down through the screen and by siphon to a constant level drain; the water level in the tray was maintained by this drain. It was ascertained with dye that the water became well mixed in the tray and uniformly distributed over the screen, and therefore over the embryos and larvae placed on it. The flow rate through the tray was not less than 50 ml/min, at which rate the velocity approaching the screen was about 1 cm/min.

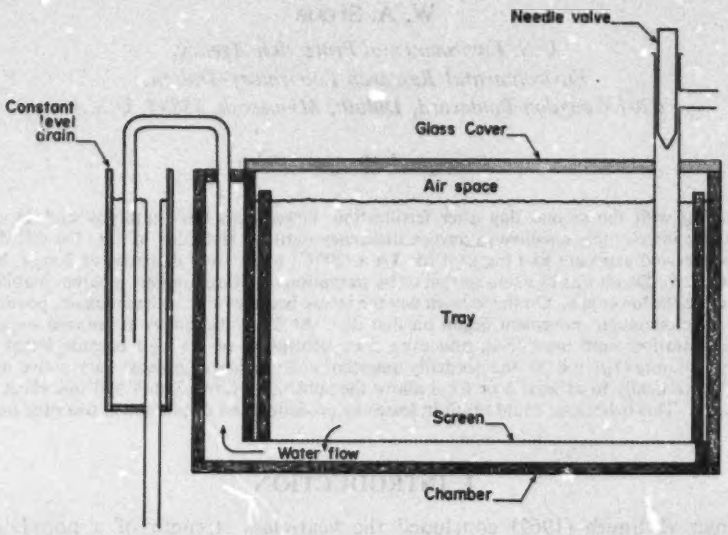

FIG. 1. Screened tray and chamber used for testing largemouth bass embryos and larvae.

The outer chamber was divided longitudinally into three separate compartments so that three trays, each with its own needle valve and drain, could be given the same treatment. A glass cover on the chamber about 1 cm above the water surface prevented air currents from disturbing the surface, but fit loosely enough that the enclosed air remained at atmospheric composition while water of low oxygen concentration was flowing through the trays. Twenty such chambers, each with three trays and distributed among four waterbaths, permitted a number of tests to be conducted simultaneously.

Similar trays, but each with a screened cover below the water surface, were used as respirometers. The water level in the chamber was raised so that the air space was eliminated; one or two trays contained larvae and the third served as a blank. A siphon from the overflow drain of an experimental or blank respirometer delivered water in a continuous stream against the cathode of an oxygen electrode connected to a meter and recorder. By this means a difference of 0·02 mg O_2/l could be read.

The water was drawn directly from Lake Superior and passed through 50-μm filters. The major inorganic constituents (approximate mean values in mg/l) included Ca, 14; Mg, 3; Na, 1·1; K, 0·5; Cl, 1·2; SO_4, 3·2; and HCO_3, 40. The pH was 7·6–7·8. The main supply to the fish was delivered continuously to a stainless steel headbox, warmed to 22° C and brought approximately to gas equilibrium with the atmosphere by vigorous aeration. A standpipe overflow maintained a constant pressure head. Aerated water was delivered from the headbox to each chamber through 6 m of 6-mm stainless steel tubing immersed in the same waterbath, and the water was brought to the bath temperature en route. The tube ended in a manifold by which water was distributed to the needle valves supplying the three trays. Except during tests of the effect of temperature on oxygen requirements, all baths were maintained at 20±0·2° C.

Water of a low dissolved oxygen concentration was obtained by mixing a continuous flow of aerated water with de-aerated water from a vacuum degassing apparatus (Mount, 1964). The proportions of the two required for a desired oxygen concentration were adjusted by use of an oxygen electrode. Once this concentration had been reached, variations from it could be kept within 0·1 mg/l by maintaining flow rates, temperature, aeration and degassing constant. All oxygen concentrations were confirmed by the unmodified Winkler method. Several different oxygen concentrations were maintained simultaneously; each was delivered continuously to a headbox fitted with an overflow standpipe to maintain a constant pressure.

Fertilized eggs were obtained from 16 spawnings at 20 or 21° C in the laboratory (Carlson, 1973) between June and October 1974 and in May and June 1975. They were removed from the spawning tanks within 6–12 h of fertilization and incubated at 20° C in aerated running water. At 20° and 8 or 9 mg O_2/l largemouth bass hatch by the third day after fertilization, swim up from the substrate on about the eighth day and start feeding by the tenth day. All references to age start with the day of fertilization; between hatching and swim-up the larvae are termed yolk-sac larvae. Groups of 12–200 embryos or recently hatched yolk-sac larvae were transferred to trays with a wide-bore pipette; the size of a group was governed by availability. The specimens were transferred in groups to keep handling to a minimum; the numbers were counted at the end of the test. After the first four spawnings the embryos were kept in the incubator through hatching, and only yolk-sac larvae were transferred to the trays. As Kramer & Smith (1962) reported, the mortality varied considerably among spawnings during the first day or two, but after hatching it was low.

Each experimental group was exposed to a reduced oxygen concentration (and in some cases to an increased temperature) for 1 to 24 h on one day during development. Before and after the exposure the test groups were maintained at $20 \pm 0{\cdot}2$° C and 9 mg O_2/l; control groups were kept at these conditions throughout. The concentration was lowered and raised by connecting the appropriate headbox with the steel tubing to the experimental chamber. The change from high to low concentration in the chamber required 10 min; from low to high, 4 min. Starting on the ninth day the fish were fed laboratory-cultured plankton and live brine shrimp nauplii. A 16-h photoperiod was maintained, with simulated dawn and dusk (Drummond & Dawson, 1970). The light intensity by day ranged from about 4 to about 25 lm, the latter occurring when the laboratory ceiling lights were on. Dead fish were removed daily. Specimens representative of each day of development, and of the effects of treatment, were examined fresh and after preservation in 4% formaldehyde. Other procedural details are considered as needed in related sections of the results and discussion.

III. RESULTS AND DISCUSSION

AGE AND SENSITIVITY TO OXYGEN DEFICIENCY

The specimens on which Table I is based were spawned on 4 June 1974; on 6 June, when they were 2 days old, they were transferred in groups of from 64 to 163 to a tray in each of nine separate chambers. Starting on that day, one group was exposed to approximately 1 mg O_2/l for 24 h on each succeeding day through the ninth, a different group each day. The fish became increasingly sensitive to oxygen lack as they approached the fifth and sixth days after fertilization; beginning with the seventh day some were able to survive the exposure.

Three subsequent spawnings were treated in the same manner but for shorter periods—series II for 6 h and series III and IV for 3 h (Table II). The sixth day after fertilization (the third after hatching) was the most critical for all three series. On days preceding and following the sixth, survival increased as the exposure period became shorter. The two series exposed for 3 h seemed especially convincing because larvae 4 days apart in age, but in different trays in the same chamber and under the same conditions, responded independently so far as survival was concerned. The

larvae in series IV were put into the trays after air-saturated water had been restored following the sixth-day exposure of the series III group, so that days 3, 4 and 5 for the younger fish were days 7, 8 and 9 for the older. In each case survival was poorest on the sixth day.

TABLE I. Percentage of largemouth bass surviving after exposure to 1±0·1 mg O_2/l for 24 h on one day between the second and ninth day after fertilization. Hatching was completed by the third day; most survivors were feeding on the tenth. Temperature 20° C

Days after exposure	Day on which exposed to 1 mg O_2/l								Control at 9 mg O_2/l
	2	3	4	5	6	7	8	9	
1	88	93	86	0	0	9	7	8	100
2	79	83	51			9	7		100
3	75	66	32			9			100
4	69	28	6						100
5	53	23	1						100
6	47	0	0						99
7	29								99
8	17								94

TABLE II. Percentage of largemouth larvae surviving until feeding after one 3-h or 6-h exposure to 1±0·1 mg O_2/l on one day between the second and ninth day after fertilization. Temperature 20° C. 57 to 157 specimens were used for each exposure

Exposure period	Series	Day on which exposed to 1 mg O_2/l							
		2	3	4	5	6	7	8	9
6 h	II	93	97	97	21	1	8		
3 h	III				99	0	15	17	24
	IV		94	94	97	3	56		

A marked abnormality appeared among some of the larvae still alive after these short exposure periods: the lower jaw appeared to become irreversibly locked in a fully opened position. These fish did not swim up, but remained on their sides at the bottom of the tray, and they could not feed. On specimens maintained until the 16th day of life the jaw was still open, very little yolk was left, and there was no food in the gut. Because this condition was seen in only one specimen among hundreds of controls and appeared frequently and regularly among the survivors of short-term exposures as well as among the asphyxiated, it was attributed to oxygen lack. Since these fish could not survive, even though alive at the end of the test, they were considered dead and subtracted from the number of survivors. Of 65 (series III) fish tested for 3 h on the sixth day (Table II), 41 were alive at the end of the test but because all had the jaw locked open survival was recorded as zero.

Growth was rapid during the larval stage, the length doubling between hatching and swim-up (Kramer & Smith, 1960), and oxygen consumption increased rapidly (Hammond, 1968), but the opercula were not well developed until the seventh day

(Carr, 1942). A possible explanation for the special vulnerability on the sixth day was sought, therefore, in measurements of oxygen consumption and growth, and in study of the development of the mouth and opercular regions.

Table III shows the mean oxygen consumption of six groups of 86 to 113 larvae in air-saturated water on each day from the fourth to the ninth, before feeding started. The oxygen electrode required a flow of not less than 20 ml/min through the respirometer, and at this rate the amount of oxygen removed by the fish was of the order of 0·1–0·2 mg/l: as a consequence the measurements varied over a considerable range. It is clear, nevertheless, that the oxygen consumption more than doubled in the period. The weight data show the daily growth of larvae from one spawning, a sample of which had been preserved each day. Oxygen consumption increased as the yolk-free weight.

TABLE III. Growth and oxygen consumption of largemouth bass larvae at 20° C on days 4 to 9 after fertilization

Day	Mean total weight* (mg)	Per cent yolk	Mean yolk-free weight (mg)	Oxygen consumption		
				µg/larva/min		µg/mg/min
				Mean	Range	Mean
4	1·4	37	0·9	0·020	0·013–0·035	0·023
5	1·6	31	1·1	0·024	0·015–0·030	0·022
6	1·7	25	1·3	0·027	0·019–0·038	0·021
7	1·9	20	1·5	0·034	0·024–0·049	0·022
8	2·1	14	1·8	0·038	0·018–0·057	0·021
9	2·4	8	2·2	0·047	0·041–0·061	0·023

*Each mean based on at least 10 preserved specimens from which excess fluid had been removed with filter paper. The amount of yolk was weighed separately on days 4 and 9 and estimated by interpolation for the intervening days, Laurence (1969) having shown that the quantity decreases approximately linearly.

The reason for the sensitivity on the sixth day may lie in the relatively late appearance of opercular movement. The lower jaw was well developed by the sixth day, and most of the larvae observed opened and closed their mouths regularly, but opercular movement was seldom seen on this day. By the seventh day, however, the opercula and rhythmic opercular movements were clearly visible. It seems possible, therefore, that by the sixth day the size and oxygen requirement had become so great the respiratory apparatus available on that day was inadequate to cope with the oxygen deficiency. The start of opercular movement on the seventh day could account for the increasing survival beginning on that day.

EFFECTS OF VARYING CONCENTRATION, TIME AND TEMPERATURE

With the sensitivity of the sixth day as an indicator, larvae from a number of spawnings were tested in experiments in which oxygen concentration and temperature, in addition to duration of exposure, were varied. The results of three such series of tests are shown in Table IV. In general, the higher the oxygen concentration between 1 and 2·5 mg/l and the shorter the exposure, the better the survival, but even at 2 mg/l a 3-h exposure caused the jaws to become locked. An important aspect of the results is their consistency. The comparable tests of series VI and VII at 1 and 2 mg/l and

TABLE IV. Numbers of 6-day-old largemouth bass larvae dead, alive but with jaw damaged, or surviving with no apparent damage after exposure to low oxygen concentrations for 1, 3 or 6 h at 20, 20·5 or 25° C

Temperature* (°C)	Dissolved oxygen† (mg/l)	Series‡	Exposure time§ (1 h)			(3 h)			(6 h)		
			Dead	Jaw damaged	Surviving	Dead	Jaw damaged	Surviving	Dead	Jaw damaged	Surviving
20	1	VI	0	0	18	1	15	0	20	0	1
		VII	0	9	15	1	15	1	22	0	0
	1·5	V				1	15	11			
	2	V				1	22	12			
		VI	0	0	23	0	3	15	0	7	5
		VII	0	0	29	0	6	14	9	3	6
	2·5	V				1	2	49			
22·5	1·5	V				13	37	1			
	2	V				3	51	0			
	2·5	V				21	19	18			
25	1	VI	1	20	0	18	0	0	16	0	0
	1·5	V				38	6	0			
	2	V				46	4	0			
		VI	0	18	0	24	6	0	21	0	1
	2·5	V				35	12	0			

*The temperature was raised from 20° C as the oxygen concentration was lowered and maintained within 0·2° C of that indicated. For all tests of series VI and VII, the increased temperature was maintained for 6 h; for series V, 3 h,

†Nominal concentration ±0·1 mg/l.

‡Series V, VI, and VIII spawned on different days.

§The actual duration was about 10 min less, the time required for the low concentration to be reached.

20° C were conducted on different dates on larvae from different spawnings, but the results were almost identical. Consistency is shown also by the graded effects of each of the variables. In the tests at 20° C and 1 mg/l, for example, the majority survived a 1-h exposure, 3 h killed very few outright but caused the jaws of most to become locked open, and 6 h killed nearly all. Increasing the temperature intensified the effects of reduced oxygen concentration; at 25° C 1 h at 2 mg/l caused the jaws to lock, and no larvae survived even 2·5 mg/l for 3 h at this temperature. Controls held at 22·5 and 25° C for 6 h developed normally.

Larvae of five other spawnings, and of series V to VII before and after the sixth day, were tested over similar ranges of oxygen concentration, time and temperature with results essentially the same as those in Tables I, II and IV. Survival of the test conditions was consistently poorest on the sixth day and better before and after it.

LARVAL BEHAVIOUR AT REDUCED OXYGEN CONCENTRATION

In addition to asphyxiation and damage to the jaw, reduced oxygen concentrations caused the usually quiescent yolk-sac larvae to become abnormally active on and above the substrate. The usual movements during normal development were of two types: an occasional twitch, by which the larva changed position, and a looping horizontal swimming movement by which it moved laterally for a centimetre or two but did not rise above the screen. In air-saturated water the larvae moved very little during the first day or two after hatching, but became more active as they neared the swim-up stage. Laurence (1972) observed similar movements. At reduced oxygen concentrations the frequency of these movements increased markedly, and a third type appeared: a vertical looping and spiralling swimming movement that carried the larva well above the screen and even to the water surface 5–6 cm above it. Here, too, the effects were graded to the oxygen concentration. At 1 and 2 mg/l and 20° C the larvae became very active immediately; even recently hatched larvae with large yolk sacs swam vertically and reached the surface. They responded less vigorously at 3 mg/l, but still swam toward the surface; at 4 mg/l movements were more numerous than at higher concentrations, but not vertical. This increased activity, especially the vertical movements, might cause larval mortality by increasing the likelihood of predation or by moving them off the nest away from fanning by the parent (Miller, 1971).

To obtain a quantitative expression of these movements, three trays were arranged so that water of different oxygen concentrations and temperatures could be introduced. About 50 three-day-old larvae were placed in each tray, and the numbers and types of movements observed in 1 min were recorded at intervals through day 7 at several concentrations and temperatures. Representative portions of the results are shown in Table V. At 20° C 4 mg O_2/l caused increased activity, but no surfacing. At 23–24·5° C even 5 mg/l caused surfacing.

The effects of oxygen concentrations as high as 4 and 5 mg/l on activity brought to mind the possibility that something other than oxygen, perhaps associated with the degassing apparatus, was responsible. Degassing did not change the pH, and it did not remove carbon dioxide; some nitrogen was removed, but this seems an unlikely stimulus. Taste and smell seem unlikely explanations also, because the increased activity continued without diminution for as long as the reduced oxygen concentration was maintained: in one case for 3 h. In view of the effect of temperature on survival

TABLE V. Effects of reduced oxygen concentration and increased temperature on activity of 4- and 7-day-old largemouth bass larvae (double horizontal lines indicate a change in oxygen concentration)

Time (h)	Tray 1			Tray 2			Tray 3		
	Temperature (°C)	Oxygen* (mg/l)	Movements†	Temperature (°C)	Oxygen* (mg/l)	Movements†	Temperature (°C)	Oxygen* (mg/l)	Movements†
				4-day-old larvae					
12.30	20	4	37	20	9	n.c.	20	9	n.c.
13.15	20	4	39	20	9	1	20	9	2
13.30	20	9	n.c.	20	4	n.c.	20	9	n.c.
13.40	20	9	4	20	4	28	20	9	1
13.50	20	9	n.c.	20	4	21	20	9	n.c.
13.51	20	9	n.c.	20	9	n.c.	20	9	n.c.
14.00	20	9	6	20	9	2	20	9	1
14.15	20	3	n.c.	20	9	n.c.	20	4	n.c.
14.30	20	3	76‡	20	9	7	20	4	21
14.35	20	9	n.c.	20	9	n.c.	20	9	n.c.
16.50	20	9	4	20	9	5	20	9	7
				7-day-old larvae					
15.35	23·5	7	6	20·2	5	5	23·3	5	n.c.
15.46	23·8	7	10	20·2	5	13	23·7	5	37‡
16.00	23·8	7	9	20·2	5	11	23·9	5	45‡
16.10	23·8	7	n.c.	20·2	5	n.c.	24·0	7	n.c.
16.20	24·0	7	15	20·2	5	3	24·0	7	15
16.30	24·0	7	13	20·2	5	4	24·2	7	14
16.34	24·0	7	n.c.	20·2	4	n.c.	24·2	7	n.c.
16.45	24·0	7	14	20·2	4	35	24·2	7	13
16.53	24·2	7	n.c.	20·2	4	n.c.	24·2	4	n c.
16.54	24·2	7	11	20·2	4	37	24·5	4	72‡
17.02	24·2	7	13	20·2	4	38	24·5	4	—‡, §

*Nominal concentration ±0·1 mg/l.
†Number of movements counted in 1 min; n.c. = not counted
‡Larvae surfacing.
§Movements continuous; too many to count.

at reduced oxygen concentrations, the marked difference in response to the same oxygen concentration associated with a 3–4 degree difference in temperature suggests strongly that the larvae were responding to oxygen deficiency. Furthermore, the usual quiescent behaviour was resumed when the oxygen deficient water was re-aerated.

IMPLICATIONS FOR YEAR-CLASS FORMATION

These results support the belief that a critical period exists in the early life history of a fish, during which it is especially susceptible to mortality (Hjort, 1926). The existence and nature of the critical period may vary with species (May, 1974), but for the largemouth bass there appear to be at least four causes of mortality during the first 2 weeks: these include damage to the nest by wave action (Kramer & Smith, 1962), desertion by the male at low temperatures (Kelley, 1968), failure to begin feeding (Carr, 1942; Laurence, 1969, 1972), and the susceptibility to oxygen deficiency described here.

Kramer & Smith (1962) found no apparent relationship between the success of a largemouth bass year-class and oxygen concentration, but since in their study the oxygen concentration did not fall below 5·8 mg/l while the embryos and larvae were on the nests it remained well above the damaging range. Oxygen concentrations in the vicinity of those tested here can occur naturally in the vicinity of largemouth bass nests, however. J. J. Peterka (personal communication) measured concentrations as low as 4 mg/l adjacent to centrarchid nests (and even 2·43 mg/l at a largemouth bass nest) between 08.00 and 09.00 h during the spawning season. Concentrations could have been considerably lower before sunrise. Since the temperatures 20 and 25° C are within the range over which largemouth bass spawn (Kramer & Smith, 1960; Clugston, 1966; Breder & Rosen, 1966), the possibility of a damaging combination of oxygen concentration and temperature is not remote.

The effect on behaviour may be potentially more dangerous to a largemouth population than asphyxiation or the locked jaw. Although most 6-day-old larvae can survive an hour at 1 or 2 mg O_2/l, the increase in activity at low oxygen concentrations is so prompt and vigorous that lowering the concentration for even a few minutes could move them from the nest. At an oxygen concentration otherwise adequate for development (Carlson & Siefert, 1974), increasing the temperature by a few degrees could have the same effect. Furthermore, the response is not restricted to the sixth day, but lasts from hatching to swim-up, which lengthens the period of vulnerability to adverse conditions.

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References

Breder, C. M., Jr. & Rosen, D. E. (1966). *Modes of Reproduction in Fishes.* Garden City, New York: The Natural History Press.

Brungs, W. A. (1971). Chronic effects of low dissolved oxygen concentrations on the fathead minnow (*Pimephales promelas*). *J. Fish. Res. Bd Can.* **28**, 1119–1123.

Carlson, A. R. (1973). Induced spawning of largemouth bass (*Micropterus salmoides* (Lacépède)). *Trans. Am. Fish. Soc.* **102**, 442–444.

Carlson, A. R. & Siefert, R. E. (1974). Effects of reduced oxygen on the embryos and larvae of lake trout (*Salvelinus namaycush*) and largemouth bass (*Micropterus salmoides*). *J. Fish. Res. Bd Can.* **31**, 1393–1396.

Carr, M. H. (1942). The breeding habits, embryology and larval development of the large-mouthed black bass in Florida. *Proc. New England Zool. Club* **20**, 43–77.

Clugston, J. P. (1966). Centrarchid spawning in the Florida everglades. *Q. J. Fla. Acad. Sci.* **29**, 137–143.

Drummond, R. A. & Dawson, W. F. (1970). An inexpensive method for simulating diel patterns of lighting in the laboratory. *Trans. Am. Fish. Soc.* **99**, 434–435.

Dudley, R. G. & Eipper, A. W. (1975). Survival of largemouth bass embryos at low dissolved oxygen concentrations. *Trans. Am. Fish. Soc.* **104**, 122–128.

Gottwald, S. (1965). Der Einfluss zeitweiligen Sauerstoffmangels in verschiedenen Stadien auf die Embryonalentwicklung der Regenbogenforelle (*Salmo gairdneri* Rich.). *Z. Fisch.* **13**, 63–84.

Hammond, B. R. (1968). The effects of incubation temperature on oxygen consumption of largemouth bass embryos and larvae. *Ann. Rep. Res. New York Coop. Fish Unit* **1**, 33–36 (Multilithed).

Hjort, J. (1926). Fluctuations of the great fisheries of northern Europe viewed in the light of biological research. *J. Cons. Int. Explor. mer* **1**, 5–38.

Kelley, J. W. (1968). Effects of incubation temperature on survival of largemouth bass eggs. *Prog. Fish. Cult.* **30**, 159–163.

Kramer, R. H. & Smith, L. L., Jr. (1960). First-year growth of the largemouth bass, *Micropterus salmoides* (Lacépède), and some related factors. *Trans. Am. Fish. Soc.* **89**, 222–233.

Kramer, R. H. & Smith, L. L., Jr. (1962). Formation of year classes in largemouth bass. *Trans. Am. Fish. Soc.* **91**, 29–41.

Laurence, G. C. (1969). The energy expenditure of largemouth bass larvae, *Micropterus salmoides*, during yolk absorption. *Trans. Am. Fish. Soc.* **98**, 398–405.

Laurence, G. C. (1972). Comparative swimming abilities of fed and starved larval largemouth bass (*Micropterus salmoides*). *J. Fish. Biol.* **4**, 73–78.

Lindroth, A. (1942). Sauerstoffverbrauch der Fische. II. Verschiedene Entwicklungs- und Alterstadien vom Lachs und Hecht. *Zeit. vergl. Physiol.* **29**, 583–594.

May, R. C. (1974). Larval mortality in marine fishes and the critical period concept. In *The Early Life History of Fish* (Ed. Blaxter, J. H. S.). New York, Heidelberg, Berlin: Springer-Verlag.

Miller, R. W. (1971). Effects of fanning on the dissolved oxygen environment and mortality of largemouth bass embryos. Ithaca, New York, Cornell University, M.S. Thesis, 118 pp.

Mount, D. I. (1964). Additional information on a system for controlling the dissolved oxygen content of water. *Trans. Am. Fish. Soc.* **93**, 100–103.

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